Implications for varying food distributions for fitness in Steller sea lions

Steller Sea Lion Research Initiative SSLRI
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Progress report (6-months)

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Summary of activities

The main aims for the period November 2001 to April 2002, were to establish a research team, develop a basic modelling approach and build a preliminary model framework. To this end, a research team was appointed. Discussions were held with a number of Steller sea lion researchers at the Vancouver marine mammal conference and with biologists at the NMML in Seattle. As a result of these discussions, a basic modelling framework was proposed and presented at an in-house seminar within the SMRU/St Andrews research group. The model is now being modified in response to points raised.

Milestones.

The project management chart defined 12 specific tasks and assigned milestones to each.

- Task 1 -Purchase computing resources.
    - Completed, computing facilities were provided.
    - **Completion date:- Month 2 Target date:- month 2**

- Task 2 -Familiarisation and establishing model frameworks.
    - A team comprising the PI, three research fellows (two biometricians and a biologist) and a graduate student was established.
    - Literature search and discussions with wide range of Steller sea lion biologists
    - Basic modelling framework developed and modified in response to wide consultation with in-house statistical and biological research groups.
    - **Completion date:- preliminary model Month 4 Target date:- month 3 + ongoing**

- Task 3 -Meetings in Anchorage and Seattle.
    - PI and one research fellow attended Vancouver marine mammal meeting for discussions with SSLRI biologists. Research Fellow visited NMML at Seattle and PI attended Anchorage SSLRI project workshop.
    - **Completion date:- Month 2 Target date:- month 2 + ongoing**

- Task 4 -Develop diving model
    - Simple diving models based on patch distribution and physiological constraints under development. General physiological models developed for marine mammal diving are being modified to account for size and age class differences in diving capabilities and prey handling constraints.
    - **Completion date:- preliminary model Month 6 Target date:- month 6 + ongoing**
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- Task 5 –Develop patch use model
- Task 6 – Develop foraging trip/haul-out model
- Task 7 –Develop energy allocation/population model.

    These three tasks have been coalesced.
    - tasks 5,6 and part of 7 are being addressed as part of an overall sea lion distribution model, based on class-specific prey profitability map. (see Appendix 1.)
    - task 7- population model. Initial work concentrating on developing models of energy acquisition and vital rates (juvenile survival, Appendix 2) and

developing a statistical model of growth to provide an update function to relate size class structure to previous size class structure and energetic state (Appendix 3)

- **Completion date:- N/A. Ongoing developments, on schedule for completion by 2nd year of project**
- **Target date:- N/A. modelling exercises to be completed within time scale of the project.**

Summary of project and model development

Various hypotheses have been put forward to explain the decline in the population of Steller sea lions, for convenience, they can be grouped under three main headings, which can be roughly stated as :-

1. Fisheries hypothesis.
Changes in prey composition due to differential fishing pressure have resulted in a decrease in foraging success of some sex and age classes of Steller sea lions. This has resulted in the observed population decline.

2. Environmental change.
Changes in prey composition due to large scale environmental change have resulted in a decrease in foraging success of some sex and age classes of Steller sea lions. This has resulted in the observed population decline.

3. Other anthropogenic/environmental effects.
Some combination of other (ie non food limitation), potential sources of enhanced mortality or reduced productivity are responsible for the observed population decline.

So far, none of these have been rigorously tested. This is probably due to a combination of the daunting prospect of collating the available data and the lack of a suitable framework in which to examine the hypotheses.

Several problems, which must be considered before attempting to test or compare these hypotheses, including:

- It is likely that some combination of all three processes are operating.
- There may well be geographical and temporal changes in the relative importance of the three processes.
- The observed effects are the declines in both pup production and total population size, both fairly coarse and often sparse measures and almost always them-selves estimates with some (potentially large) error.
- The available data on other mortality causes is weak.
- Hypotheses 1 and 2 are effectively the same from the sea lion's perspective. They both address the question: could the observed changes in prey availability have caused the observed effects.
- We are not qualified to assess the relative probability that the observed changes in prey resulted from anthropogenic or natural environmental changes.

In order to make progress, we aim to address the more general question, which underlies both the fisheries and environmental change hypotheses. i.e. Are apparent changes in prey distribution and abundance sufficient to explain the observed population effects?

To address this we need to be able to say something sensible about each of the following linkages.

- How does the species and size composition of the prey affect the diet. ie what is the functional response.
- How does the geographical and vertical distribution of prey affect foraging success.

- How do sea lions distribute themselves between prey patches.
- How does foraging success affect the energetic status of each size and/or sex class.
- How does energetic status affect the growth patterns, the short term and longer-term reproductive success and the survival of sea lions.
- How do changes in these vital rates affect population dynamics.

Modelling approach

Prey – diet. To actually parameterise the functional response would require an experimental set up beyond the scope of this project. In the absence of a fully parameterised functional response we will attempt to reduce the description of the prey field. Diet studies suggest a wide/catholic diet, in some areas.
So we make the simplifying assumption that prey choice may be influenced by the profitability of each available prey type. We can then derive some aggregate value for the prey assemblage, at any point on the map, based on a description of the horizontal and vertical distribution of the prey species, some basic assumptions about the value and local cost of feeding on each type.

Overall value of different prey items can be estimated as a function of the XYZ location, nutritional value and handling cost. This can be done for both species and size classes within species. These values will clearly vary for different size and behavioural classes of sea lions. E.g. even large, high density patches of deep living, large prey may be unavailable to post weaning pups, alternatively widely dispersed low density prey patches of small shallow species may be available but insufficient for lactating females. We will therefore incorporate simple descriptions of behaviour and diving abilities for each sex and size class of sea lions, to assign travel and diving costs to each location.

Clearly there are many assumptions implicit in this analysis. In terms of sea lion biology, perhaps the most important is the suggestion that different sizes of sea lions will have different capabilities and constraints. This is the essence of the cost function and drives the estimate of local prey value. Differences in capabilities relate primarily to changes in swimming costs and diving capacities with body size. These will be investigated through appropriate models of diving and swimming behaviour.

Differences in constraints are primarily related to haulout behaviour. E.g. Breeding sea lions are constrained to remain on, or regularly return to, fixed haulout sites, whereas non-breeding sea lions are not as obviously constrained, although behavioural data indicates that they regularly return to haulout sites. These differences in constraint may influence how different classes of sea lions assess the profitability of a particular location and influence how different classes distribute themselves.

FORAGING SUCCESS

Developing maps of the profitability surface for each sea lion class will be a major undertaking, but if successful, the framework will provide a tool to allow us to examine the effects of altering the prey field. An investigation of how different classes of sea lions will respond to different prey fields will again be a major sub project. This requires the development of simple foraging behaviour models to estimate energy gain from different prey distributions. Models will incorporate descriptions of behaviour in patchy environments, where strategies of patch residence will be influenced by patch quality, energetic requirements of pups, recent resource acquisition and level of stored resources. Then, for each size/sex/reproductive class of sea lions we can examine effects of changing prey field characteristics by altering prey composition and looking at foraging success and energetic state of hypothetical animals.

POPULATION EFFECTS

To this point we have only been interested in the development of models to describe the likely effects of prey distribution on foraging success. The next step of converting these analyses into predictions of the likely effects on population processes will be the most difficult.

We will address these issues in two, hopefully converging exercises.

In one we will use available data to attempt to relate various population parameters to the predictions of our models of foraging success (Appendix 2).

In the other we will generate a size/age class structured population model which will use energetic input at each size class to predict movement between reproductive and survival states (Appendix 3). These exercises will proceed in parallel, with the results of exercise one being used to fine tune the overall size/age structured population model.

In the initial model specification phase, we have identified a series of under-pinning assumptions which need to be examined in depth and may require us to develop specific modules.

Specific assumptions to be investigated/sub models to be developed.

1. Spatial setup
    a. *Assumption*--Haulout positions (both breeding and non-breeding) remain fixed over time. *Data available on haulout distribution and some data on numbers at each. Preliminary examination of haulout location information and historical count data support the basic assumption. Relative attractiveness of a site will be allowed to vary, but can be modelled as a function of prey availability.*

2. Resource map.
    a. *Assumption*--Prey distribution is known or statistical properties of prey distribution are known. *For specific areas (e.g. Kodiak) such data are currently being generated. Models will be designed to accept these data. Majority of available data is at a coarse scale relative to the sea lion haulout and movements data. Major effort to extract if possible.*
    b. *Sub-model* --The prey content of a spatial location can be condensed into the value of a single resource index. *Combine information on biology to assess the gross value, eg total energy content modified by any info we can get on handling and/or capture costs to give a net value of each prey type. Then produce overall gross value of a location.*
    c. *Sub-model* --Relationship between sea lion state and value of resource index for locations with the same prey composition.

3. Cost function
    a. *Sub-model* --State-specific cost of travel between locations. *Size linked cost of swimming, state related constraints on foraging ranges.*
    b. *Sub-model* --State-specific cost of diving. *Models of dive capabilities and prey*

handling constraints being developed.

c. *Sub-model* --State-specific predation risk. *Almost total absence of information. Can play with different predation patterns as part of a sensitivity analysis. May be much more important than previously thought.*

4. Spatial distribution of seals.
   a. *Sub-model* --Profitability of a location is defined as the difference between resource content and cost.
   b. *Assumption* --Seals track the profitability of locations. *Needs some experimental or observational data to validate.*
   c. *Sub-model* --Imperfect knowledge of the environment. *It is plausible that knowledge is:- A function of age, and may therefore be class specific, e.g. Could be simple –naïve V omniscient. Or more complex based on previous history; A function of distance from the haulout? Could possibly incorporate rules about when to settle on a patch as result of encounter history; A function of the rate of environmental change.*
   d. *Sub-model* --Haul out process effects. *Are there state dependent differences in haulout behaviour.*

5. Population processes .
   a. *Sub-model* --Age and condition of seals are necessary for the model. *Few data. How to use sparse data from unrepresentative sections of the population to make inferences about the rest of it.*
   b. *Sub-model* --State-specific survival as a function of food intake. *Little information. Separate exercise to extend elephant seal models to sea lions.*
   c. *Sub-model* --State-specific growth as a function of food intake. *Needs developing, but should be relatively simple.*
   d. *Sub-model* --State-specific fecundity as a function of food intake.

6. Model fitting.
   a. Data/model-fitting for energetics.
   b. Actual seal distributions. SMRU involvement in sat tagging work could be important. Maybe try to influence where and when tags are applied.
   c. Fitting parameters for population processes.

Appendix 1. Preliminary model framework.

Low-resolution map and a single haulout are currently used for trial simulations

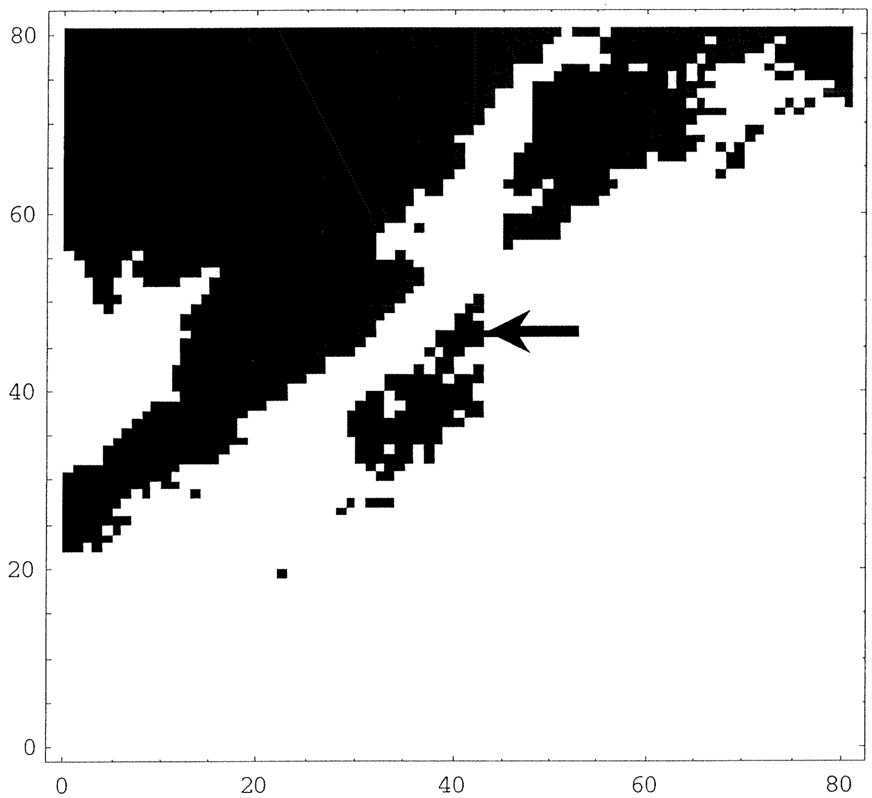

Fig. 1

1. Initially focusing on Kodiak Island, using a low-resolution map.
2. Only one haulout represented for now.
3. Many haulouts and higher resolution maps will increase computation time considerably.

Biological distances from the haulout

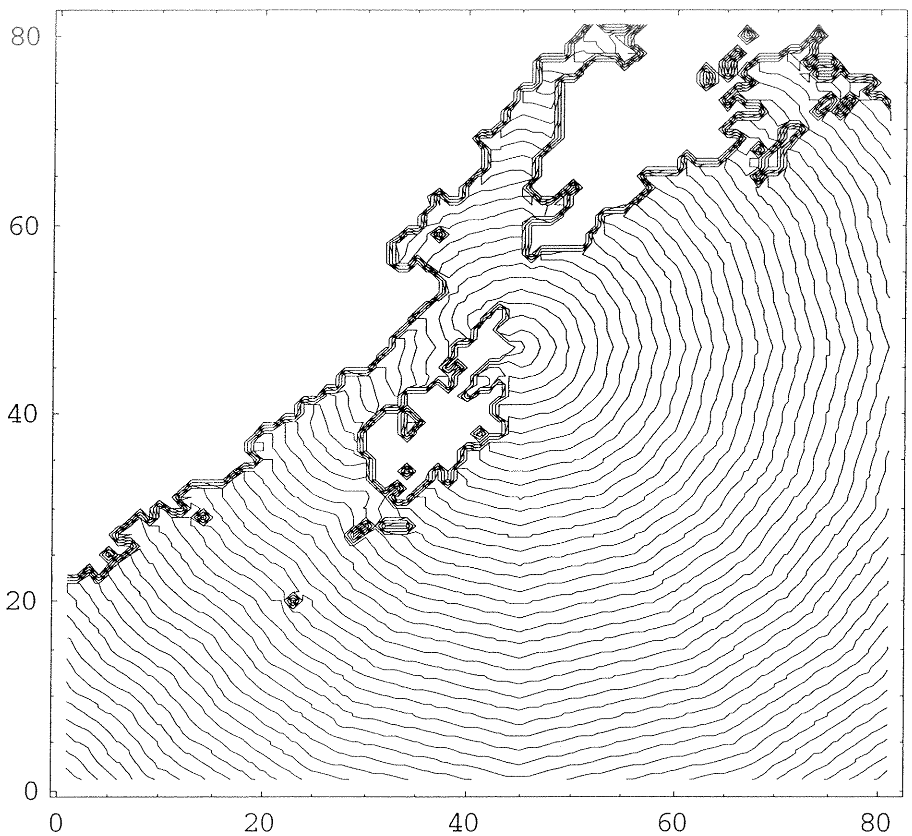

Fig. 2

- Cost function
- Cost(|class) = f(distance, depth)
- Cost defined as the energetic cost of feeding at a particular distance from a haulout. This is influenced by fidelity to haulout sites. For central place forager, cost related to distance but for a nomad, cost may not be.
- Cost described as energetic cost of travel, but may be more complex, e.g. Predation risk.

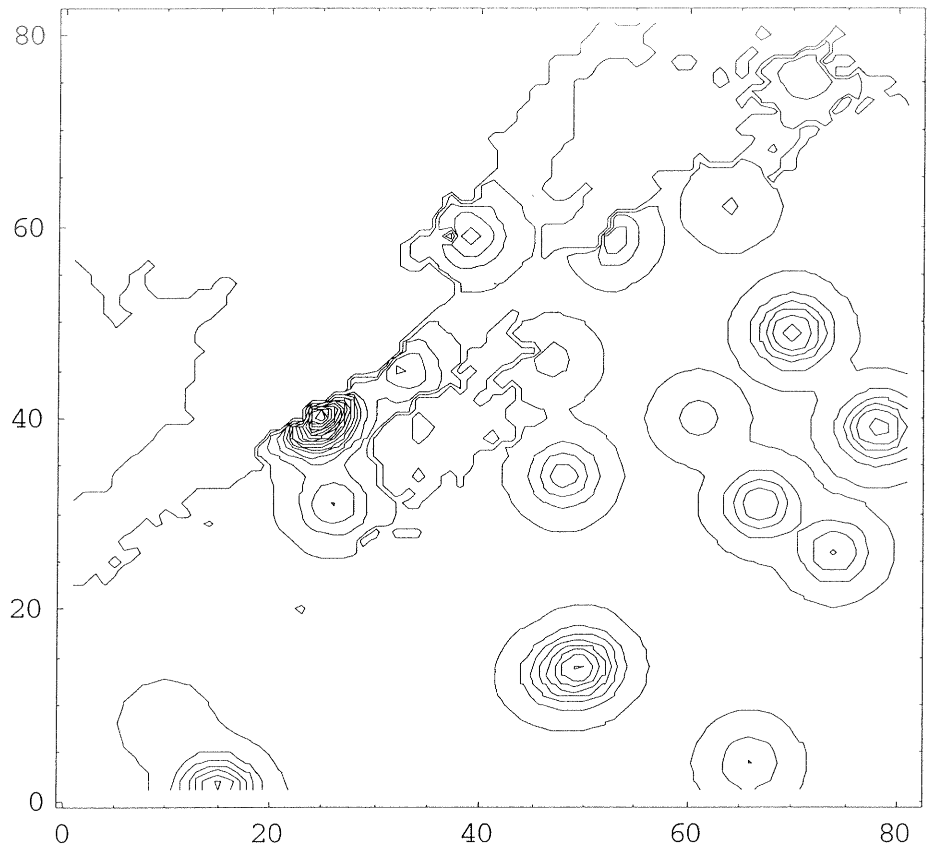

Fig. 3. **Synthetic map of productivity (standing resource availability)**

Need to summarise "prey field" into a single energetic currency that is "understood" by the sealion. That is, the full description of the prey field is collapsed to a two dimensional map of local value, i.e. the productivity minus the cost of foraging, taking into account the energetic value, size and vertical distribution of the prey at each location. This map will be class dependent, i.e. there will be a separate map for each sea lion class.
Seals belonging to different classes (defined by variables such as size, age, sex……) Will compete for resources. State of the resource at a location will change according to the predation effort.

Class-specific cost surface and the resulting profitability surface for animals of different classes

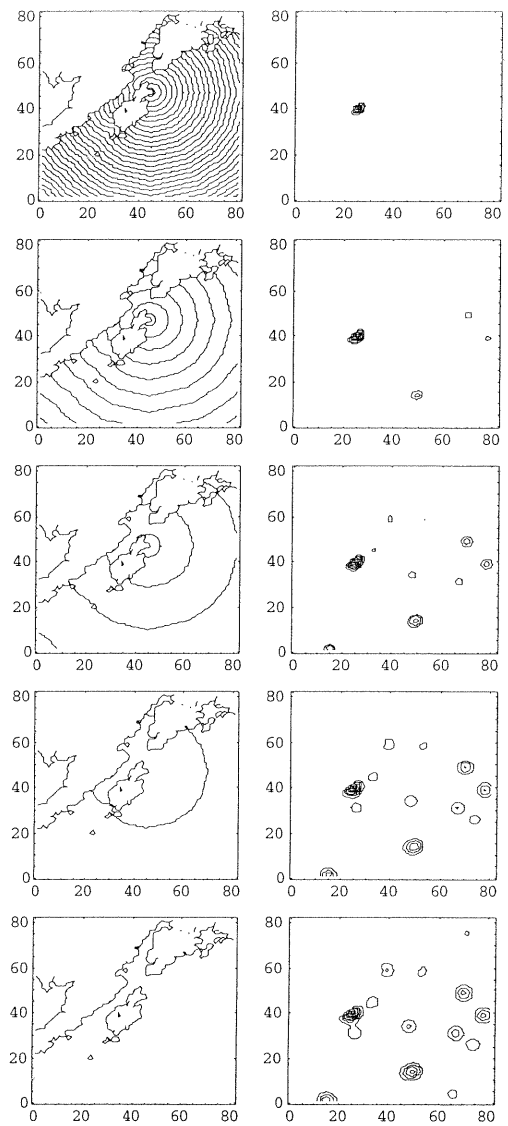

Figure 4

Class specific contour maps of the profitability of foraging at a particular location.

PROFITABILITY(class,x) = PRODUCTIVITY (x) - COST(class,x)

Individuals from classes attempt to distribute their foraging effort "ideally" according to profitability, which changes in response to effort of other classes.

This allows us to estimate class specific, per capita energy intake.

Which links to condition $\Rightarrow$ influences fecundity, survival etc. $\Rightarrow$ drives population model.

Evolution of population structure

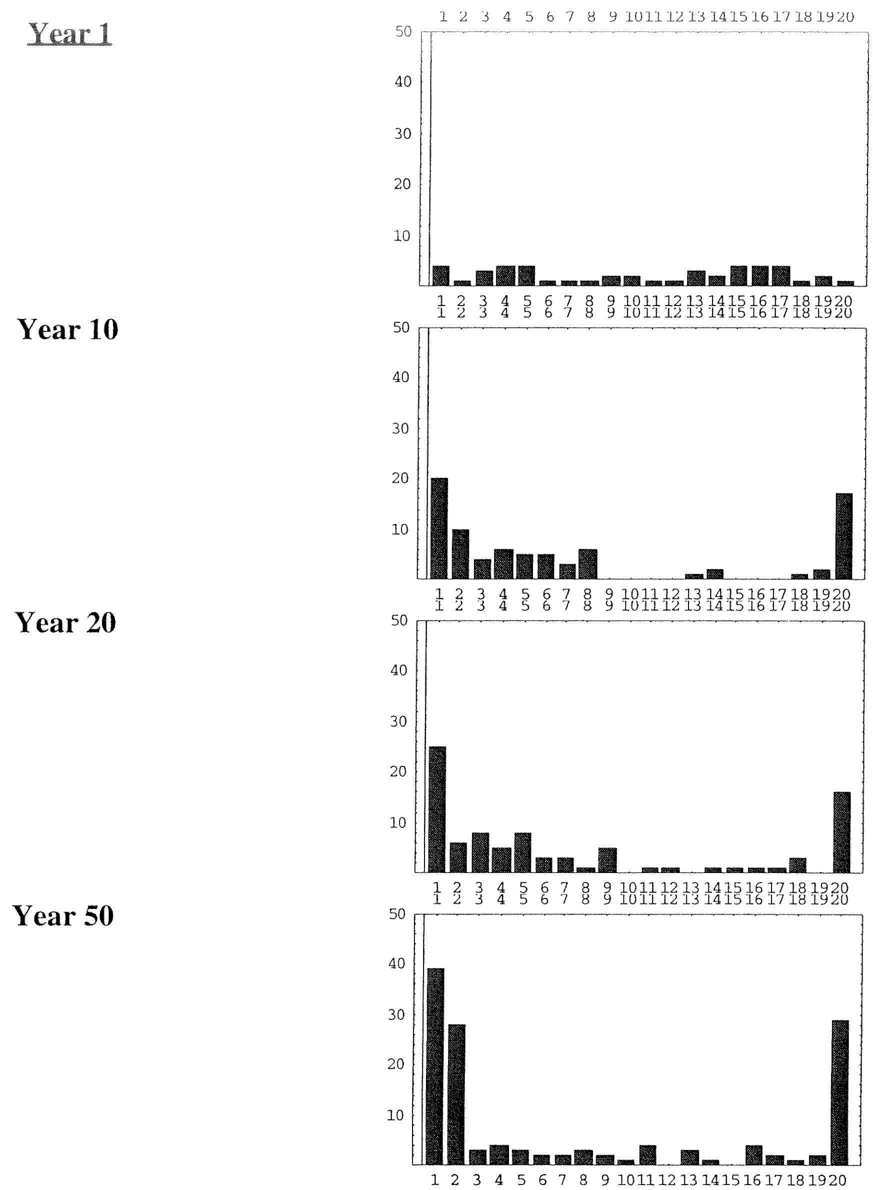

Fig 5. An example of how the age/size class structured population will respond to the energy intake defined in the previous example prey field.
This is an arbitrary example, chosen with 20 size classes and arbitrary assumptions of conversion of condition to vital rates

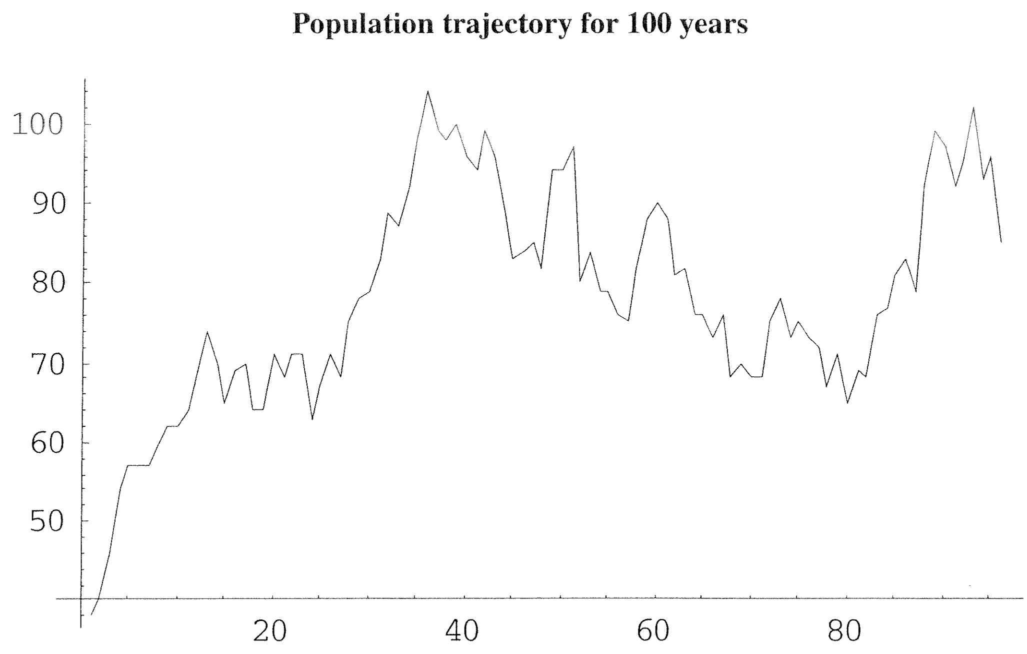

Fig. 6 Example of a 100 year population trajectory. This is a fictitious population based on the arbitrarily chosen prey field and conversions of energy to vital rate effects, used in figures 4 and 5.

The aim is to show the full scope of what we intend to do.
The approach can be summarised as combining models of :-

1 Energetics of 3D movements
2 Spatial interactions between sea lions and their prey.
3 State related impact of energy intake on demographic parameters
4 Long term population consequences.

Lack of data at several stages of this process, means that the most important aspect of this project will be a series of sensitivity analyses.

Appendix 2 Foraging success and vital rate parameters.

Models of vital rate parameters (survival/ growth/recruitment/fecundity) as function of prey acquisition.

As pup/juvenile survival has been identified as one of the prime factors in the population dynamics of sea lions we will address this issue first and attempt to model pup/juvenile survival as a function of maternal resource allocation and prey encounter rates.

Initial model developed and tested using pup weaning mass and survival data from a simple capital breeder, the southern elephant seal (Mirounga leonina). The aim is to investigate the underlying mechanism relating the resources available at weaning to juvenile survival. First models will test the hypothesis that for naïve foragers, the simplest possible foraging behaviour models may explain a large proportion of the variance in survival. This will incidentally provide a means of differentiating between the effects on survival of different aspects of environment quality. This model will be subsequently extended to incorporate maternal foraging success during lactation

Model developed assuming simple target requirement for surviving an initial critical period (e.g. when developing foraging strategy, or searching for profitable habitats). Target modified by some aspect of body condition at weaning or at independence.

A plausible and parsimonious model of foraging assumes that the initial foraging pattern comprises a series of random movements between randomly distributed food patches. So, the pattern of encounters with food would be generated by a Poisson process. Thus, if the average rate of encounters is **λ**, the probability of obtaining some target food requirement R (food items/patches) in a fixed time **t,** given an allocation of resources **X** at weaning is simply:

$$P_{survival} = \left(1 - \sum_{r=1}^{r=R-(1+X)} \frac{(\lambda t)^r e^{-\lambda t}}{r!} \right) S$$

where S represents survival of mortality factors independent of weaning resource level.

This initial model was fitted to data on birth mass, weaning mass, and pup survival available for southern elephant seals breeding on Macquarie Island (54^0 37' S, 158^0 53' E). The maximum likelihood fit of the model to pooled survival data for 3 cohorts is shown in figure 7. Likelihood ratio tests indicated a significant difference between asymptotic survival (i.e. not moderated by weaning resource levels) in two years (figure 8) and between prey encounter rates in two years.

Initial model development is promising, and indicates that relatively simple models may adequately describe foraging, at least for simple capital breeders. The next stage will be to develop models further to account for maternal foraging during lactation and maternal influences on pup foraging strategies to provide a more accurate description of sea lions behaviour.

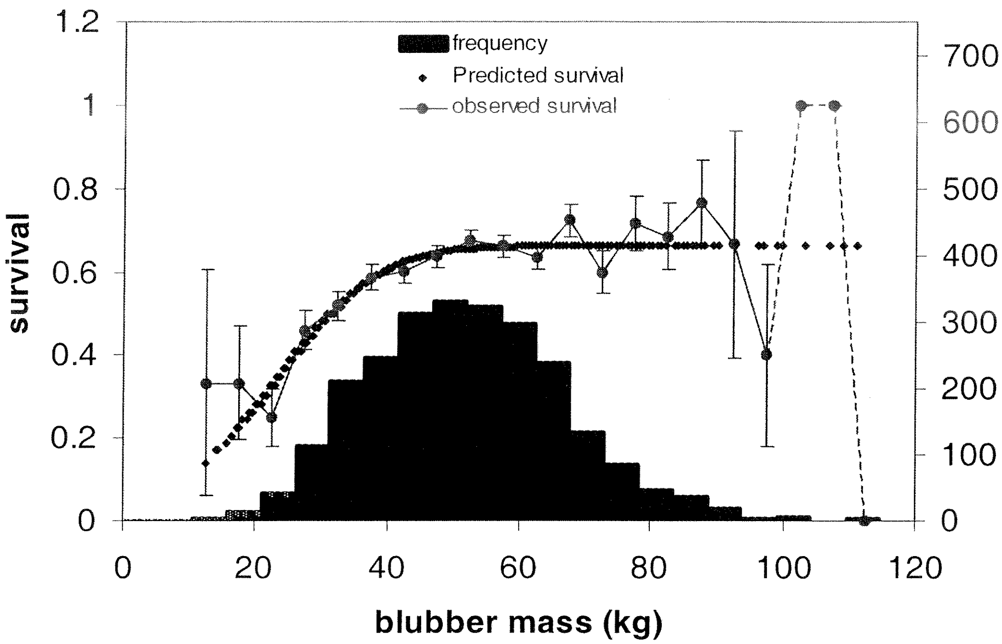

Figure 7. Survival V estimated weaning energy stores in southern elephant seal pups.

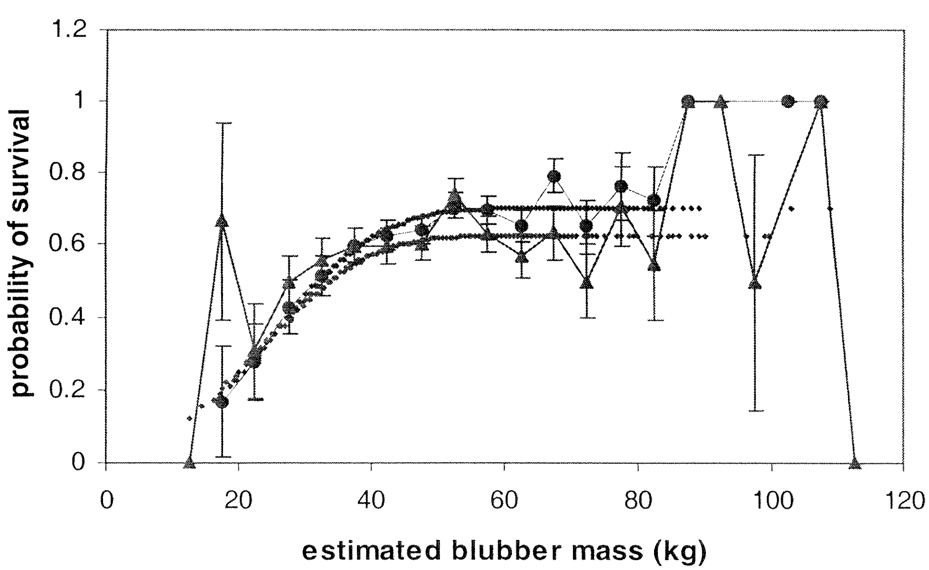

Figure 8 Survival V estimated weaning energy stores for two cohorts of southern elephant seal pups. Asymptotic survival (not related to body condition at weaning) was shown to be significantly different between years.

STELLER SEA LION PROJECT UPDATE

DR CRISTIANA K. LETTERI

1. Models of Population Dynamics

We propose a framework for modelling the population dynamics of Steller sea lions from a methodology developed in [2]. This is a state space model for defining population dynamics models (the state process) and measurements (the observation process). The state process consists of a number of population sub-processes. The product of the sub-process matrices is a Leslie matrix ([5], [6]).

A model of biological growth is used to update the population size structure. This is useful for a number of sub-processes including breeding and survival. [9] apply a MCMC state space approach to model population dynamics in fisheries.

2. Modelling Biological Growth

[1] performs a statistical analysis of a sample of size measurements from a Steller sea lion population. [3] consider growth models in a bioenergetic framework. We adopt the von Bertalanffy model of biological growth to derive an update for the population process in the methodology developed in [2].. [8] provides a comprehensive review of alternative growth models.

3. The Method of successive approximations

We assume that the von Bertalanffy is the process underlying biological growth in the population. We derive a contraction mapping for the population size structure update process. This is instrumental in solving the growth function with minimal parametric assumptions. By the method of successive approximations ([4]), we find the fixed point of the update process.

4. Future Developments

The model for updating the population size structure derived from the method of successive approximations will be implemented in a Windows application (in Visual C++).

One issue to be resolved is how to classify animals in the population in a way that is meaningful to the population dynamics approach developed. The space of quaternions will be investigated as a possible framework for working with the parameters in the classification scheme.

The review of growth models in [8] provides a useful source of alternative growth specifications for the size structure update process. The Richards model ([7]) receives favorable reviews in the biological growth literature ([3], [1]). An alternative update process with the Richards growth model could be tested on available data on Steller sea lions available through the Alaska Department of Fish and Game, Anchorage ([1, p. 501]).

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